

Multivoltinism and Usage of Multiple Nest Substrates in a West Texas Sand Dune Population of *Pseudomasaris phaceliae* Rohwer (Hymenoptera: Vespidae: Masarinae)

JOHN L. NEFF AND ALLAN W. HOOK

(JLN) Central Texas Melittological Institute, 7307 Running Rope, Austin, Texas 78731, USA;
email: jlnatctmi@yahoo.com

(AWH) Department of Biology, St. Edward's University, Austin, Texas 78704-6489, USA;
email: allanh@stedwards.edu

Abstract.—A west Texas population of *Pseudomasaris phaceliae* was found to be multivoltine and active from April to September. Unlike previous reports of nests constructed only on stones, nests were commonly constructed on the stems and infructescences of its host plant, *Phacelia integrifolia*. Emergence data indicated the primary sex ratio is strongly female biased (53:14). Nest parasitism was rare, but predation was common. Data on nest architecture, nest construction, and foraging behavior are presented.

Pseudomasaris is the only North American genus of the Masarinae, a relatively small (300+ spp.) but widespread clade of pollen and nectar provisioning vespids wasps (Carpenter 1982, 2001, Gess 1996). Torchio (1970) reported in considerable detail on the biology of *Pseudomasaris edwardsii* (Cresson) but little is known of the biology of the remaining 14 species. Brief reports on nest structure and/or nest sites have been published for eight of these species, including *Pseudomasaris phaceliae* Rohwer, but only floral records are available for four other species, and nothing at all has been published on the biology of the remaining two.

During a brief visit to Monahans Sandhills State Park in June 2005, we encountered a large population of *Pseudomasaris phaceliae* visiting flowers of *Phacelia integrifolia* Torr. (Boraginaceae). *Pseudomasaris phaceliae* is an infrequently collected but sometimes locally abundant species of the arid American Southwest (Arizona, New Mexico, west Texas, and adjacent Mexico) (Richards 1966, and pers. obs.). Although previous reports had indicated that *P.*

phaceliae, like most other *Pseudomasaris* species, constructs its nests on stones (Parker 1967, Torchio 1970), we found that at Monahans, *P. phaceliae* was commonly attaching its nests to plant stems, and only rarely to stones. In addition, *P. phaceliae*, like most other temperate masarine species, had previously been assumed to be univoltine (Parker 1967, Gess 1996), but wasps emerged in early July from a nest collected during June suggesting multivoltinism. This prompted a series of visits to this site to gather additional information on the nests and behavior. Follow-up trips were made in July, August, and September 2005 and April, May, June, and August 2006.

Habitat.—Monahans Sandhills State Park (32.128° N, 103.953° W) is located in Ward County, Texas on the southern edge of a large dune field of quartz-rich Quaternary sands that stretch northward into southeastern New Mexico (Machenberg 1984, Muhs 2001). While much of the dune field is partially stabilized by shin oak (*Quercus havardii* Rydb.) and other perennials, large moving dunes are common in



Figs. 1-2. 1. *Pseudomasaris phaceliae* nest (indicated by arrow) on *Phacelia integrifolia* stem. 2. Incomplete *P. phaceliae* nest with one completed cell and one cell under construction.

the Park. Soils in the sandhills consist almost exclusively of loose sands. Occasionally, winds expose the underlying caliche layer, but generally there are no rocks or stones in the dunes beyond those brought in for the caliche service roads. Like most of Texas, summers are warm with July maximum temperatures averaging 35 C. Rainfall is low, averaging 33.6 cm per year, with 75% of precipitation occurring during a six-month May to October summer/fall period. Despite the relative aridity, the water table is quite shallow in the sand hills due to an underlying impermeable caliche layer. Water-loving plants like *Salix nigra* Marshall (Salicaceae) and *Baccharis salicina* Torrey & A. Gray (Asteraceae) are found in some of the deeper depressions among the dunes where temporary ponds may form following unusually heavy rains (Machenberg 1984).

Nests.—Although a few nests were found on miscellaneous plant stems (such as a sapling of *Prosopis glandulosa* Torr. (Fabaceae) or stems of the erect herb *Mentzelia strictissima* (Wootton & Standl.) J. Darl. (Loasaceae), the vast majority of the nests we found were on stems or infructescences of larger (over 40 cm high) individuals of *Phacelia integrifolia* (Fig. 1.). Nests were located at heights of 20.3–71.1 cm above the ground ($n=50$, mean = 41.0 ± 9.9 cm). Typically there was only one nest per plant although a few plants had two, and one *Phacelia* plant had four nests, two older nests from which emergence was complete, and two newer nests under construction.

Like those of other *Pseudomasaris* species, nests consisted of one or more cylindrical cells attached lengthways one to another (Torchio 1970). Cells of nests on plants were always positioned with the long axis

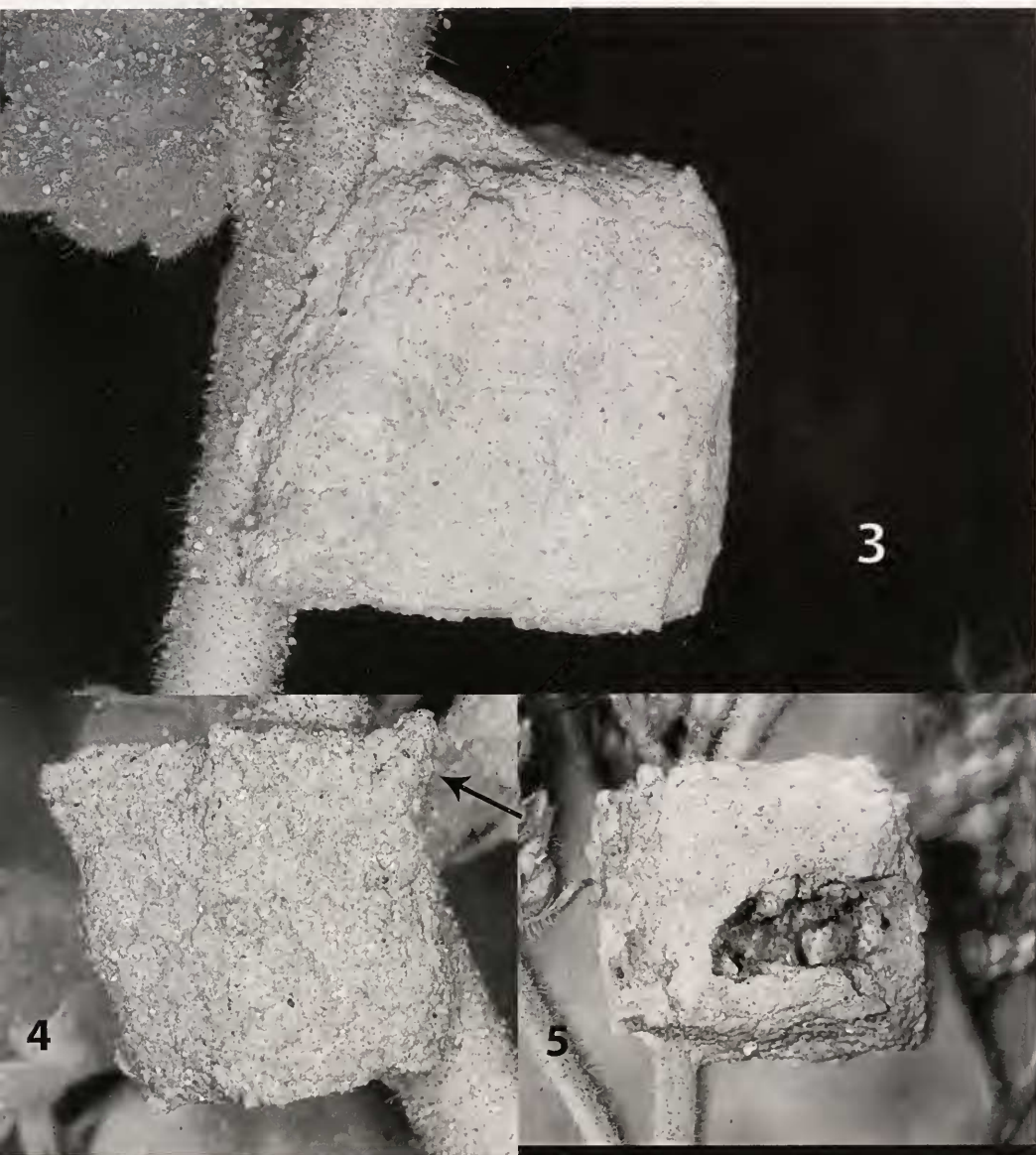
oriented vertically, regardless of the orientation of the stem or infructescence (Fig. 2). Nests on plants averaged 5.4 ± 3.8 cells per nest, (1–14, $n = 53$), a value that probably underestimates the true number of cells per nest since some of the nests may not have been complete when censused. Nests on stems were initiated by laying down a strip of the sand-soil mix along a stem or infructescence. The female then constructed the hemispherical inner end of the cell at the upper end of the strip, and completed the cell wall by adding irregular strips or scale-like patches of the moist sand-soil mix. Upon returning with a sand-soil load, the female inserted her head in the nest and curled her metasoma so its tip was opposite her head. The moist sand-soil mix was added to the cell wall by simultaneously working the mix from within with her mandibles and tapping it from the outside with the flattened, hirsute surface of metasomal sternite 6. Time on the nest depositing cemented sand was typically brief (0.6–2.9 min).

The first cell is a true cylinder as the walls are complete, the plant substrate not being used as part of the cell wall (Fig. 2). Additional cells are attached to the walls of the initial cell so the nest grows in an asymmetrical manner away from the stem rather than around it (Fig. 3). Cell walls are rather thin, only 0.4–0.5 mm thick, but quite strong. Nests within 100 meters of the caliche road were usually constructed with a mix of relatively coarse sand particles (0.1–0.4 mm in diameter), and much finer (0.02–0.04 mm) particles, presumably caliche dust. Nests further from the road are constructed of sand alone. The particles are bound together with regurgitated nectar, and perhaps, glandular products. As there was no free water in the dunes, nectar (or perhaps honey-dew) was the only likely source for the bulk of the liquid used to moisten the sand-soil mix. Nest fragments placed in water softened but were still intact after being immersed for 48 hours, suggesting substances be-

yond just sugar may be holding the walls together. These moistened nests quickly sprouted fungal hyphae, the fungi presumably growing on the nectar sugars. In contrast, the true mud nest walls and partitions of nests constructed by *Trypargilum politum* (Say) or *Osmia lignaria* (Say) dissolve almost instantly when placed in water (pers. obs.).

Individual cells were 15.2 ± 1.2 mm (12.8–17.6, $n = 19$) mm long with an average diameter of 4.2 ± 0.2 mm (3.8–4.5, $n = 28$). The distal end of the cell was hemispherical while the cell opening was simple and truncate. After provisioning, each cell was closed with a cemented sand plug 0.5–0.8 mm thick medially and 1.0–1.3 mm thick at the sides. Additional sand and fine particles were added to the nest exterior as construction proceeded, filling the spaces between the cells (Fig. 9). In one unfinished nest in which the second cell was only half finished, soil had been added along the juncture of the two cells, strengthening their connection, although additional soil had not been added elsewhere to the outer surface of the first cell. Upon completion, the nest has flattened, relatively smooth walls concealing the outlines of individual cells. We found no indication of empty spaces between the cells. Completed nests on stems usually lacked obvious ornamentation but a few (4 of 50) had conical projections on the margins of the nest (Fig. 4).

Females were commonly observed collecting fine soil particles along the caliche road (Fig. 6) and, less frequently, in the dunes. Females would hover 10–15 cm above the soil surface and repeatedly drop to collect sand or soil. We did not obtain a complete picture of soil collection but it was clear that during most bouts on the soil surface, the wasps did not add nectar to the soil surface prior to collection. Rather, they used their mandibles and foretarsi to add soil or sand to a moist soil bolus held behind the mandibles by their modified labial palpi. Regurgitated nectar

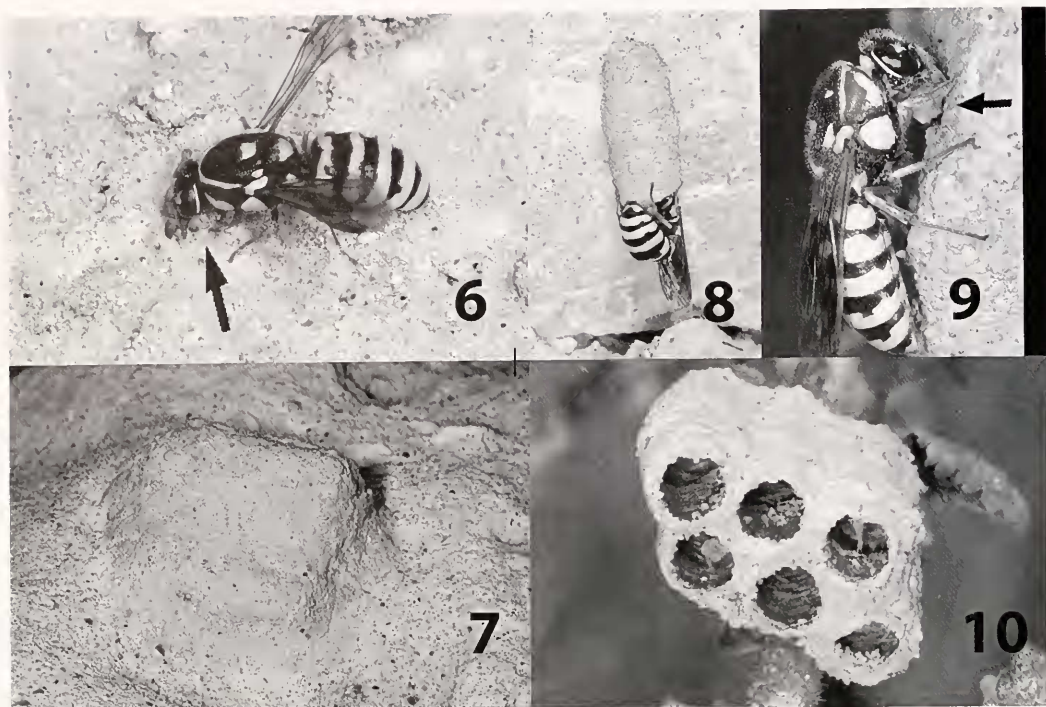


Figs. 3–5. 3. Completed *Pseudomasaris phaceliae* nest showing asymmetrical position on *Phacelia integrifolia* stem. 4. Ornamented *P. phaceliae* nest (projection indicated by arrow). 5. *P. phaceliae* nest opened laterally, probably by birds.

is apparently added to this bolus while the wasps are hovering. As in *Pseudomasaris edwardsii*, females constructing cells or adding sand to the nest exterior typically made long trips (20–30 min duration) to gather nectar at flowers as well as sand, interspersed between series of 3–4 relatively short (0.9–3.1 min) trips. The latter trips

were presumably for sand only since they were too brief to allow for both sand and nectar collection.

While the majority of nests were constructed on plant stems, some nests were constructed on small stones brought in for a caliche service road through the dunes. These were structurally similar to the nests



Figs. 6–10. 6. *Pseudomasaris phaceliae* female collecting sand (sand bolus indicated by arrow). 7. Completed *P. phaceliae* nest on stone. 8. Female extending walls of new *P. phaceliae* nest. 9. Female adding sand (indicated by arrow) to exterior of *P. phaceliae* nest. 10. Emergence holes from six-celled *P. phaceliae* nest.

constructed on stems, but had fewer cells, never more than three, averaging only 1.3 ± 0.5 cells (1–3, $n = 28$). While all the stem nests were constructed during the year in which they were discovered, many of the rock nests were worn and/or damaged and may have been constructed in prior years. Unlike the situation in stem nests, the first cells constructed on stones were usually not true cylinders as the stone was used as part of the cell wall. The first cells constructed typically were attached to the stone along their entire length (Fig. 8), although in a few cases, only the basal half of the cell was attached to the substrate, with the outermost portion arching away. Completed nests on stones often appeared to be triangular in cross-section, due to the smoothing of the sides and the addition of soil, which greatly widened the base of the nest (Fig. 7). Nests on rocks occurred both on the sides and upper surfaces without any consistent orientation. Completed

nests on stones were quite cryptic as the outer nest covering matched the color of the pale stone on which they were constructed. Nests on *Phacelia* plants were more conspicuous since the pale nests contrasted with the green stems or young infructescences, but the nests were still somewhat cryptic since the infructescences, leaves and/or leaf tips all commonly turn brown with age.

Nests are provisioned with a dense mass of regurgitated pollen-nectar pellets. The pellets had short projections and were oriented so the projections, rather than the main mass of the pellets, contacted the cell walls. Pellets averaged 0.6–0.7 mm across with projections from 0.2 to 0.6 mm long. Unlike the provisions of *Pseudomasaris edwardsii*, the innermost face of the provision mass of *P. phaceliae* was not smoothed so the individual pellets were easily distinguished. The outer face of the provision mass (the surface facing

the cell closure) was smooth and convex. We found several cells being provisioned, and others with feeding larvae but recovered only a single cell with a completed, intact, provision mass. This mass was 15.2 mm long, occupying nearly all the cell, leaving a small open space of 0.8 mm between the mass and the roof of the hemispherical inner end, and 1.6 mm between the mass and the cell closure.

Host Plant and Foraging.—*Pseudomasaris phaceliae* is believed to restrict its foraging to flowers of *Phacelia* spp. (Torchio 1970). At Monahans dunes, individuals of *P. phaceliae* foraged only at flowers of *Phacelia integrifolia*, the only *Phacelia* species flowering. *Phacelia integrifolia* is a widespread annual of the American Southwest, occurring on a variety of rocky or sandy substrates, particularly gypsum or limestone (Correll and Johnston 1970). The plants bear scorpioid cymes of small, pale purple flowers. In west Texas, flowering occurs primarily from March through May (Correll and Johnston 1970), although herbarium records from the Plant Resources Center of the University of Texas, Austin, Texas, show flowering as late as the end of July in the Monahans Sandhills area, and a non-technical guide indicates flowering through September (Ajilvsgi 2003). *Phacelia integrifolia* was common and in flower during our first 2005 visit to Monahans dunes on 16 April, although cold, wet weather prohibited any observations of floral visitors. When we revisited Monahans Dunes on 18 June 2005, we found *P. integrifolia* flowering was still widespread although most abundant in certain depressions between the dunes. When the site was revisited a month later in July, most *P. integrifolia* plants on the dunes were brown and dead, and flowering was restricted to the large plants occurring in the depressions between the dunes. Unlike the typical, erect plants on the dunes and most other habitats (Fig. 1), these plants were sprawling and multi-branched, almost shrub-like in aspect, with

greatly enlarged stems. These depression plants were still strongly flowering when the site was revisited in August. On the final 2005 visit on 16–18 September low levels of flowering were still occurring among the large depression plants although most plants were dead, and flowering was limited to a few inflorescences. On 21 April 2006, *P. integrifolia* was flowering and locally abundant on the dunes, but surprisingly, was absent in the depressions where the large, long-flowering individuals were found in 2005. Flowering continued, with a gradual decline in overall abundance through May and June 2006. By August 2006, only secondary inflorescences of the few surviving individuals were still flowering.

Individual flowers of *Phacelia integrifolia* begin opening around 0830 CDT (approx. 2 hrs after sunrise), and flowers continue opening through the day. Individual flowers last approximately two days. Anthers dehisce fully shortly after flower opening, and are usually stripped of pollen within two hours of opening. Some larger bees, such as species of *Habropoda*, *Osmia*, or *Martinapis* began foraging on *P. integrifolia* at or before 0800 early in the season, but *Pseudomasaris phaceliae* was always a late starter. Females were rarely observed before 0830 CDT and they were generally not active until after 0930 CDT with air temperatures above 30 C. Foraging continued until sundown, although females were sometimes observed resting on stems or branches during periods of peak heat in late afternoon (air temperatures above 39 C).

Foraging rates recorded on 13 July 2005 were quite rapid, perhaps a reflection of the high temperatures (33–35 C) and resource depletion due to the high number of wasps and bees concentrated on the relatively few *Phacelia* plants still flowering. Wasps visited an average of 24.5 ± 5.3 (16.4–31.2, $n = 20$) *Phacelia* flowers per minute. Nectar visits were quite quick, averaging only 0.8 ± 0.3 (0.3–2.0, $n = 40$)



Figs. 11–12. 11. *Pseudomasaris phaceliae* female collecting pollen of *Phacelia integrifolia*. 12. *P. phaceliae* female nectaring at flower of *P. integrifolia*.

seconds per flower while pollen-collecting visits were longer at 4.1 ± 3.0 (1.1–11.2, $n = 20$) seconds. During a foraging bout, the proportion of flowers worked for pollen was low, averaging only $13.7 \pm 14.6\%$ (0–41.7, $n = 20$). This is presumably a reflection both of the low availability of fresh flowers with available pollen, and the fact that some foragers were constructing their nests and not foraging for pollen at the time. If we exclude foraging series where no flowers were visited for pollen, the proportion of flowers visited for pollen rises only slightly to $19.6 \pm 13.7\%$ (3.4–41.7, $n = 14$).

A nectar foraging bout involved landing on medial portions of the exerted staminal filaments and rapidly inserting the remarkably extensible proboscis (~ 4.5 mm long when fully extended) to reach the nectary at the base of corolla tube (Fig. 12). The initial approach to a flower presumably involved some assessment of pollen availability, since foraging behavior changed when a pollen forager encountered a flower with obvious available pollen. A pollen forager would grasp the staminal filament near the anther with her hind and mid-tarsi while hovering (Fig. 11). She would then grasp an anther with her

mandibles and extract pollen by scraping pollen to her mouthparts with the tarsal brushes of her forelegs. Depending on pollen availability, a wasp might work several anthers on a flower before moving down the filaments to insert her mouthparts to gather nectar.

A female observed on 17 June 2006 took 8.40 hrs and 15 foraging trips to provision a cell. Pollen foraging appeared to commence immediately after oviposition. Because of poor light conditions, we were not able to determine if the female deposited an initial pollen and nectar load immediately after ovipositing as has been reported for *Pseudomasaris edwardsii* (Torchio 1970). Pollen trips averaged 31.53 ± 7.10 min (19.32–41.72, $n=13$) and deposition time in the nest between trips averaged 2.06 ± 0.48 min (1.50–3.52, $n=14$). As noted for *P. edwardsii* (Torchio 1970), the female rotated within the cell during the later phases of pollen deposition as she deposited pollen pellets.

Development and Voltinism.—Only fragmentary data were obtained on development. The only intact egg recovered was smooth, slightly asymmetrical, and 3.7 mm long with a medial width of 1.0 mm. The posterior end of the egg was attached

Table 1. Collection dates for nests of *Pseudomasaris phaceliae* from Monahans Sandhills with emergence dates and sex ratio of the wasps.

Nest	Collection date	Emergence date	Males	Females
H-1	16-vi-2005	by 12-vii-2005	1	14
N-1	18-vii-2005	19-vii-2005	0	2
N-2	18-vii-2005	23-vii-2005	0	1
N-3	18-vii-2005	3-iv-2006	0	1
N-4	15-viii-2005	28-viii-2005	1	3
N-5	15-viii-2005	1-ix-2005	0	1
N-6	18-vii-2005	19-iv-2006	0	2
05-06	18-vii-2005	approx. 3-iv-2006	0	1
05-07	18-vii-2005	approx. 3-iv-2006	1	1
05-02	18-vii-2005	18-iv-2006	2	0
06-01	23-iv-2006	26 to 29 iv-2006	1	5
06-02	19-v-2006	1 to 7 vi-2006	1	8
06-03	18-vi-2006	27-vi to 11-vii-2006	1	7
06-04	18-vi-2006	1 to 7 vii-2006	4	3
06-05	18-vi-2006	5 to 11 vii-2006	1	3
06-06	18-vi-2006	12-vii-2006	1	1
Total			14	53

perpendicularly to the inner surface of the cell wall, just below the hemispherical, inner end of the cell. The ventral surface of the egg, which paralleled the flat inner surface of the provision mass, was somewhat flattened, but the dorsal surface of the egg arched slightly into the curved space of the hemispherical inner cell cap. In two instances where late instar larval feeding was noted, the larva fed along the side of the provision, eating its way down the provision mass toward its distal end. Sometime after completing feeding, the larva spun a thin, translucent cocoon that adhered tightly to the cell wall. Defecation occurred after the completion of the cocoon. Feces were typically deposited as an irregular ring of smooth, flattened, semi-spherical pellets (0.8–1.0 mm wide, and 0.5–0.6 mm tall), around the inner end of the cell, although some of these are sometimes pressed into a flattened cake with unrecognizable individual pellets. Nest dissections indicated wasps overwinter as prepupae. Adults emerge by chewing through the nest plug (Fig. 10).

The total number of generations per year of *Pseudomasaris phaceliae* at Monahans is unknown but at a minimum it is two and

perhaps as many as four. *Pseudomasaris phaceliae* was active at Monahans for at least 93 days (18 June to 18 September) in 2005 and 116 days (26 April to 19 August) in 2006. Judging from the extensive wing wear of females collected in June of 2005, the phenology of *Phacelia integrifolia*, and the emergence times of *P. phaceliae* in the lab (Table 1.), flight at Monahans during 2005 probably began in early April suggesting a flight period in excess of 156 days in 2005.

Emergence patterns of wasps from nests collected in 2005 and 2006 are indicated in Table 1. All nests collected before July had their inhabitants emerge that same year, but for nests collected in July or later, some emerged the same year but others went into larval diapause and emerged the following April. The instances of late 2005 (July to September) emergence were from nests taken from infructescences on relatively fresh green plants, and it is clear that they had been provisioned in 2005. *Phacelia integrifolia* stems usually break down completely over the winter and the glandular epidermis, to which the nests are frequently attached, falls away soon after the plant dies. It is probable that over-wintering

nests fall from the disintegrating plants and spend the winter in the sand.

Mating and Sex Ratio.—Males of *Pseudomasaris phaceliae* were observed to forage for nectar at plants of *Phacelia integrifolia* and patrol *P. integrifolia* inflorescences, but mating was not observed. Newly emerged males confined with newly emerged female nest mates attempted to mount their sisters, although it was not determined if mating was successful. Females were much more common than males at flowers at all times during our visits, and the sex ratio of wasps emerging from nests was heavily female biased 3.8:1 (53 females/14 males, Table 1). In all cases where emergence order was determined, males emerged from the first provisioned cell(s) of a nest.

Nest Associates and Predators.—Nest parasitization was uncommon. One female *Chrysurissa densa* (Cresson) (Chrysididae) emerged on 18 July 2005 from a *Pseudomasaris phaceliae* nest and a second female emerged from a different nest on 13 September 2005. *Chrysurissa densa* apparently is a specialist on *Pseudomasaris*, since besides *P. phaceliae*, its only known hosts are four other *Pseudomasaris* species. In addition, its range mirrors that of *Pseudomasaris* (Bohart and Kimsey 1982). The only other nest parasites were 10 females and 2 males of an unidentified *Monodontomerus* sp. (Torymidae) which emerged from a cell of another nest of *P. phaceliae*. As parasite emergence occurred only two days after collection of the nest, it was clearly the result of field, rather than laboratory, infestation.

Indications of nest predation were occasionally encountered. Several nests observed in 2005 and 3 of 21 nests measured in June 2006 had all their cells opened laterally (Fig. 5). The cells in these nests contained empty cocoons but had intact cell caps. Birds are the most likely predators although we cannot rule out small mammals. A small, unidentified woodpecker was seen perching and searching on *Phacelia* stems, but actual nest predation

was not confirmed. Additionally, two newly provisioned cells were encountered with small lateral slits, possibly the results of bird probes. One of these probed cells contained a larva and partially consumed pollen mass while the other was being raided and emptied by ants.

We found no indication of empty (closed but unprovisioned) cells in *Pseudomasaris phaceliae* nests at Monahans. Empty cells have been invoked as an anti-parasite defense strategy for *Pseudomasaris vespoidea* (Cresson), in which roughly 30% of the nest cells are empty (Tepedino et al. 1979).

DISCUSSION

Our observations of *Pseudomasaris phaceliae* at Monahans suggest this species has a broader behavioral range than previously observed in *Pseudomasaris*. The most obvious differences from previous reports are the incidence of multivoltinism and use of plant stems for nest placement. Multivoltinism has not previously been reported in *Pseudomasaris* and appears to be rare in the Masarinae, at least among temperate zone species (Gess 1996). Presumably, this is true because these wasps are typically oligolectic (or at least have a narrow range for floral hosts) and the flowering periods of their floral hosts usually are quite temporally restricted. Multivoltinism is possible at Monahans because of the unusual extended flowering of its floral host in this distinctive habitat, allowing a flight season that can extend from April into September in favorable years. However, it is possible that multivoltinism occurs in other non-dune populations of *P. phaceliae* associated with *P. integrifolia*. We have collected *P. phaceliae* on this species at other west Texas sites in June. Wing wear indicated these wasps were relatively newly emerged even though the few flowering *P. integrifolia* plants at these sites were in very poor condition and most plants in the populations were dead or fruiting.

As we encountered neither flowering *Phacelia* nor *Pseudomasaris phaceliae* during

July, August, or September visits to Monahans prior to 2005, multivoltinism may be a facultative phenomenon for *P. phaceliae*. The wasps could use environmental cues such as temperature and humidity, which may predict extended *Phacelia* bloom, to "determine" whether to pupate and emerge immediately or proceed to diapause. Increasing humidity, a predictor of flowering in desert plants, has experimentally been shown to be an important cue in breaking diapause in *Macrotera portalis* Timberlake (Andrenidae), a desert bee with extended diapause (Danforth 1999), while temperature (above or below 29 C) determines whether *Nomia melanderi* Cockerell (Halictidae) pupates and emerges immediately or proceeds to diapause (Stephen 1965). Even in years with extended *Phacelia* flowering, flowering declines greatly late in the year. The observation that some larvae in late provisioned nests (July or later) pupate and emerge immediately while others diapause until the following spring suggest a bet-hedging strategy predicated on the decreasing chances of encountering adequate floral resources late in the year.

Published reports have indicated that surfaces of rocks are the preferred nest substrates utilized by six *Pseudomasaris* species (Hicks 1929, Hungerford 1937, Parker 1967). In Torchio's 1970 glasshouse study, *Pseudomasaris edwardsii* females constructed nests on a variety of substrates, but not plant stems. However, the use of bamboo stakes as a nest substrate in Torchio's study suggests they may occasionally use twigs or plant stems under natural conditions. The only report on *Pseudomasaris texana* (Cresson) indicates it constructs its nests on twigs (Bequaert 1940). *Pseudomasaris vespoideis* has repeatedly been reported constructing its nests on twigs or plant stems (Cockerell 1913, Davidson 1913, Hicks 1929, Bequaert 1940, Torchio 1970), although it also is known to use rocks (Hicks 1927). *Pseudomasaris marginalis* (Cresson) was found to nest in

beetle borings in logs at a high altitude site in Colorado (Dorr and Neff 1982) although this report has been questioned (Gess 1996). In the only previous report on the biology of *P. phaceliae*, rock surfaces were the only reported nest substrate (Parker 1967).

Since rocks are rarely encountered in the Monahans Sandhills, it is not surprising that most of the *Pseudomasaris phaceliae* nests we encountered were attached to plants. The relative advantages of rock surfaces and plant stems as nest substrates are unclear. Rock surfaces are obviously more permanent and stable than herbaceous plant stems, but the importance of this difference is not clear for wasps like these that do not reuse their nests. The issue of difference of substrate permanence could easily be erased by using the stems of perennials, although *P. phaceliae* does not seem to regularly do this at Monahans. If heat stress is a problem, a strong possibility in a habitat like Monahans Sandhills where soil surface temperatures regularly exceed 40° during the late spring and summer, constructing nests well above the soil surface on plant stems might be advantageous relative to building nests on low, exposed rock surfaces.

The nest biology of most *Pseudomasaris* species is poorly known, often based on only a single population, and, in some cases, a single nest. When the biologies of more populations of more species of *Pseudomasaris* are known, it will be interesting to see if other *Pseudomasaris* species are similarly flexible in their patterns of voltinism and/or nest substrate usage.

ACKNOWLEDGEMENTS

We thank the Texas Parks and Wildlife Department (Scientific Study Permit 27-05) and the staff at Monahans Sandhills State Park for the opportunity to study the Monahans *Pseudomasaris* population. Beryl B. Simpson (The University of Texas) improved early drafts of the manuscript. Sarah Gess and an anonymous reviewer made many useful comments on the submitted manuscript.

LITERATURE CITED

- Ajilvsgi, G. 2003. *Wildflowers of Texas, revised edition*. Shearer Publishing, Fredericksburg, Texas. xix + 524 pp.
- Bequaert, J. 1940. Notes on the distribution of *Pseudomasaris* and on the foodplants of the Masaridinae and Gayellinae (Hym., Vespidae). *Bulletin of the Brooklyn Entomological Society* 35: 37-45.
- Bohart, R. M. and L. S. Kimsey. 1982. Chrysididae in America North of Mexico. *Memoirs of the American Entomological Institute* 33: 1-266.
- Carpenter, J. M. 1982. The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). *Systematic Entomology* 7: 11-38.
- . 2001. Checklist of species of the subfamily Masarinae (Hymenoptera: Vespidae). *American Museum Novitates* 3325: 1-40.
- Cockerell, T. D. A. 1913. *Pseudomasaris* bred in California. *Proceedings of the Entomological Society of Washington* 15: 107.
- Correll, D. S. and M. C. Johnston. 1970. *Manual of the Vascular Plants of Texas*. Texas Research Foundation, Renner, Texas. xv + 1881 pp.
- Danforth, B. N. 1999. Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*. *Proceedings of the Royal Society of London, B* 266: 1985-1994.
- Davidson, A. 1913. *Masaria vespoidea*. *Bulletin of the Southern California Academy of Science* 12: 17-18.
- Dorr, L. J. and J. L. Neff. 1982. *Pseudomasaris marginalis* nesting in logs in Colorado (Hymenoptera: Masaridae). *Pan-Pacific Entomologist* 58: 124-128.
- Gess, S. K. 1996. *The Pollen Wasps. Ecology and Natural History of the Masarinae*. Harvard University Press, Cambridge, Massachusetts. x + 340 pp.
- Hicks, C. H. 1927. *Pseudomasaris vespoidea* (Cresson), a pollen provisioning wasp. *Canadian Entomologist* 59: 75-79.
- . 1929. *Pseudomasaris edwardsii* Cresson, another pollen provisioning wasp, with further notes on *P. vespoidea* (Cresson). *Canadian Entomologist* 61: 122-125.
- Hungerford, H. B. 1937. *Pseudomasaris occidentalis* (Cresson) in Kansas (Hymenoptera - Vespidae). *Journal of the Kansas Entomological Society* 10: 133-134.
- Machenberg, M. D. 1984. *Geology of Monahans Sandhills State Park, Texas*. Bureau of Economic Geology, The University of Texas at Austin. 39 pp.
- Muhs, D. R. and V. T. Holliday. 2001. Origin of late Quaternary dune fields on the Southern High Plains of Texas and New Mexico. *Geological Society of America Bulletin* 113: 75-87.
- Parker, F. D. 1967. Notes on the nests of three species of *Pseudomasaris* Ashmead (Hymenoptera: Masaridae). *Pan-Pacific Entomologist* 43: 213-14.
- Richards, O. W. 1966. New records of *Pseudomasaris* Ashmead (Hymenoptera: Vespoidea, Masaridae), with notes on *P. phaceliae* Rohwer and *P. cazieri* R. M. Bohart. *Proceedings of the Royal entomological Society, London (B)* 35: 47-55.
- Stephen, W. P. 1965. Temperature effects on the development and multiple generations in the alkali bee, *Nomia melanderi* Cockerell. *Entomologica Experimentalis et Applicata* 8: 228-240.
- Tepedino, V. J., L. L. McDonald, and R. Rothwell. 1979. Defense against parasitization in mud-nesting Hymenoptera: Can empty cells increase net reproductive output. *Behavioral Ecology and Sociobiology* 6: 99-104.
- Torchio, P. F. 1970. The ethology of the wasp, *Pseudomasaris edwardsii* (Cresson) and a description of its immature forms (Hymenoptera: Vespoidea, Masaridae). *Los Angeles County Museum Contributions in Science* 202: 1-32.